REPRODUCTIVE BEHAVIOUR AND POLYANDRY IN A SMALL INSULAR POPULATION OF SPOTTED SANDPIPERS IN NEWFOUNDLAND

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Reproductive Behaviour and Polyandry in a Small Insular Population of Spotted Sandpipers in Newfoundland

by

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Abstract

A small insular population of nesting Spotted Sandpipers (Actitis macularia), estimated at 38-45 individuals, was studied during the summers of 1979 and 1980. Daily observations were made from late May when birds first arrived through mid-July when most eggs had hatched. Some individuals were colour banded or otherwise marked. During the two seasons 31 nests were located and histories resulting from daily observations at these nests are summarized. Contrary to reports of some researchers (e.g. Oring & Knudson 1972), perceived size differences and plumage markings in this population did not allow reliable determination of sex in the field. Extensive observations were made at nests where one or both individuals were marked to determine whether one or both pair members participated in clutch and brood tending activities. Marked individuals were also followed when off the nest to assess use of feeding areas. Of 14 marked females, two were known to mate with multiple males and some details of these relationships are presented. Aggression was rare and seemed to occur primarily in situations where existing pair relationships were challenged or in instances of "mate defense." Territorial behaviour by males and

females was not apparent and overlapping feeding areas were observed. Theoretical arguments which suggest selective pressures for incubation and brood tending by one member of a breeding pair are reviewed and their relevance to the Spotted Sandpiper mating system are discussed.

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Introduction

Polyandry is a rare mating system among birds and has been observed in less than 1% of species studied (Lack 1968; Jenni 1974; Oring 1982). In its most general usage polyandry implies a mating system in which a female has multiple mates in one reproductive season (Maxson & Oring 1980). Its occurrence has attracted considerable theoretical interest (Orians 1969; Trivers 1972; Jenni 1974; Graul, Derrickson & Mock 1977; Wittenberger 1979; Oring 1982) owing to anomalies associated with these mating systems, i.e., males have an increased role in parental care and females tend to be larger and more aggressive than males (Jenni 1974). These and other related factors have made the study of polyandry useful for understanding relationships between sexual selection, sex role, sexual dimorphism, patterns of parental care and a possible role of sex ratio in the evolution of mating systems.

The study of mating systems covers a broad range of topics as indicated by the definition suggested by Emlen and Oring (1977:222): mating system for a population refers to "the general behavioral strategy employed in obtaining mates." It encompasses such

features as: (i) number of mates acquired, (ii) manner of mate acquisition, (iii) presence and characteristics of any pair-bonds and (iv) patterns of parental care provided by each sex.

Attempts to define and classify mating systems have relied heavily on the concept of pair-bonds (Orians 1969; Selander 1972; Brown 1975; Wittenberger 1979). Jenni (1974) suggested that most vertebrate mating systems can be classified in terms of the number of individuals with which one individual forms pair-bonds. The utility of this pair-bond concept for classifying mating systems has been limited because of difficulties in establishing an operational definition of the term, differences in pair-bonding relationships across species and a lack of detailed observations on pair-bonding behaviour.

Several alternative criteria for classifying mating systems have been suggested. Emlen and Oring (1977) described how mating systems might be categorized according to the ecological and behavioural potential of individuals to monopolize mates and the means through which monopolization takes place. However, these ecological models have continued to use pair-bonding relationships in distinguishing between

certain mating systems (see Oring 1982). Alternatively, some authors have suggested that the most relevant classification for mating systems would be made on the basis of genetic criteria: i.e., which individuals contribute gametes to which zygotes (Trivers 1972; Ralls 1977; Wade & Arnold 1980). Such information is however extremely difficult to collect in the field (Trivers 1972).

Spotted Sandpipers (Actitis macularia) were one of the first avian species documented to practice polyandry on the basis of observations of individually marked birds (Hays 1972). These small shorebirds of the family Scolopacidae breed throughout much of North America. Mating strategies employed by individuals of this species are flexible (Jenni 1974; Oring & Maxson 1978), and both monogamy and polyandry may occur in the same breeding population (Oring 1979). Polyandrous females typically mate with and produce a clutch for each male in succession and share incubation and brood tending care only with the last male (Hays 1972).

Among polyandrous species a distinction is commonly made between what have been called simultaneous and sequentially (or serially) polyandrous systems (Hays 1972; Jenni 1974; Graul et al. 1977;

Oring & Maxson 1978; Wittenberger 1979; Oring 1982). This distinction is based on the way which pair-bonds are formed and maintained. In simultaneous polyandry, pair-bonds between a female and her multiple males overlap in time, whereas pair-bonds in sequentially polyandrous species are thought to be formed in succession without overlap. Serial polyandry is more typical among Spotted Sandpipers (Hays 1772; Oring & Knudson 1972), although simultaneous matings have been reported (Oring & Maxson 1978). Such distinctions are complicated by lack of a criteria with which to measure the strength and duration of pair-bonding. Pair-bond characteristics may also vary considerably among species, making comparative interpretations difficult. Quantitative and qualitative data on bonding relationships are still needed for many species.

Information about Spotted Sandpiper mating systems has come from two primary sources. (1) Hays (1972) reported serial polyandry in a small individually marked population breeding on an island in New York. (2) Oring and Knudson (1972) reported their observations of two small populations of Spotted Sandpipers in Minnesota: one breeding in a marsh habitat and the other breeding on an island. In their

marsh population clutch loss from predation was high, females demonstrated an impressive capacity to replace clutches and matings were essentially monogamous. The island population was estimated to have less clutch predation, a sex ratio skewed towards more males (relative to the marsh population) and some females which mated with multiple males.

Oring and Knudson (1972) felt that some differences between their marsh and island populations exemplified factors promoting the occurrence of polyandry. Spotted Sandpipers may have evolved a capacity for producing multiple clutches in response to high predation, as observed in the marsh population, and longer breeding seasons in the southern latitudes where they nest. Island populations may experience less predation and as a related consequence have a higher proportion of breeding males (Oring & Knudson 1972). Females with a capacity to produce multiple clutches might mate with additional males when they are available and replacement clutches are not needed.

Subsequent work has shown that the sex ratio for the Minnesota island population of Spotted Sandipers is balanced, however, sex ratio may be functionally skewed by certain aggressive females competitively excluding

other females from breeding. Hays (1972) reported that the sex ratio for her island population was skewed towards excess males.

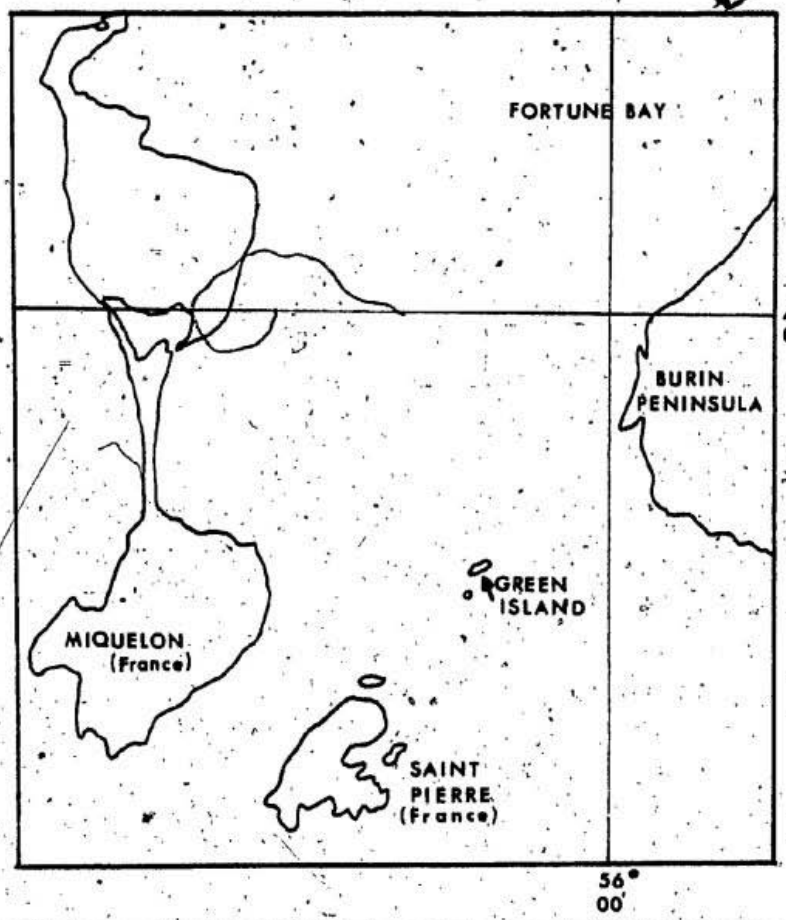
Female Spotted Sandpipers are generally described as having more heavily spotted breast markings and being larger than males. Careful reading of the literature, however, suggests some disagreements as to the magnitude of these differences (e.g., Hays 1972, Oring & Knudson 1972; Emlen & Oring 1977; Maxson & Oring 1980). Surprisingly little has been published on actual measurements for estimating size for this species (Maxson & Oring 1980). Such measurements are critical in establishing the best estimators of size for this species, in documenting suggested differences and in generating confidence intervals for predictions of sex when other independent sexing criteria are not available. Some differences in sexual dimorphism reported for this species could be due to geographic variation, and the importance of this factor is evaluated in the present study. In addition, sexual dimorphism in Spotted Sandpipers has been attributed to sexual selelction (Emlen & Oring 1977) and quantitative measurements would allow for comparisons with other polygamous species where sexual selection is involved.

The present study developed primarily from an interest in discovering how widespread and general polyandry is among Spotted Sandpipers. In an attempt to maximize the probability of finding polyandry, a small island on the southern coast of Newfoundland, Canada, known to regularly support a breeding population of Spotted Sandpipers and to be free of terrestrial predators, was selected as a study site. An attempt was made to collect information about general ecology, reproductive behaviour and social organization that would allow for comparisons with other Spotted Sandpiper populations already studied. Information about sex ratio, extent of sexual dimorphism, instances of predation and pair-bonding relationships were of special interest. It was initially assumed that some reasonable estimate of sex ratio could be obtained by visually examining birds as this procedure had earlier been used (Oring & Knudson 1972). Such evaluations were studied in comparison with behavioural observations (copulations) and quantitative measurements. Observations of pair-bonding relationships were studied to attempt to distinguish between sequential and simultaneous matings for this species.

Study Area and Methods

Green Island (45-53 N, 56-Ø W), situated at the entrance to Fortune Bay, Newfoundland, lies 4.8 nautical miles west of Point Crewe, Burin Peninsula (Figure 1). The island is oval measuring about 1,ØØØ m in length and about 45Ø m at its widest extent, with an area of 3.8 ha. The island is bordered by an area of large rocks which vary in exposure depending on tide and sea conditions. The interior of the island is characterized by gently sloping hills which reach highest elevations of 42 m and 25 m at the east and west ends respectively (Figure 3). There are no trees or shrubs on the island and the primarily grassy vegetation rarely exceeds 1 m in height. In addition to Spotted Sandpipers, a large colony of Leach's Storm-Petrels (Oceanodroma leuchorhoa), Savannah Sparrows (Passerculus sandwichensis labradorius), a pair of Common Ravens (Corvus corax) and a pair of Great Black-backed Gulls (Larus marinus) nest on the island. The Canadian Coast Guard maintains a manned light station on the island. With the exception of two dogs maintained by the lightkeepers, no other terrestrial vertebrates are known to inhabit the island.

Figure 1. A map of Green Island at the entrance to Fortune Bay, Newfoundland. From Canadian Hydrographic Service Nautical Chart No. 4016.


FORTUNE BAY
47°
00'
BURIN
PENINSULA
GREEN
ISLAND
MIQUELON
(France)
SAINT
PIERRE
(France)
56°
00'

In 1979 and 1980, field work began in late May, when birds first arrived, and continued through mid-July when most eggs had hatched. To monitor sandpiper activity and locate nests, one to four daily walks around the island's perimeter were made following an existing path from which all portions of the island were visible. During surveys all Spotted Sandpiper sightings and behaviour (location, movements, displaying, copulations, vocalizations, feeding, aggression, brood tending, etc.) were recorded. Surveys were timed and designated check points established to standardize this procedure. Observations were made with 7x35 and 10x50 binoculars and recorded on cassette tapes. Weather conditions were noted at regular intervals throughout the day. When not conducting surveys I remained at regular observation points near nests with marked individuals and recorded movements and other activities. Individuals which behaved as a pair (e.g., feeding in close proximity, nest searching, displaying, courtship flights, copulations, etc.) were scrutinized for apparent differences in size and degree of spotting pattern on breast whenever possible. Such pairs were often subsequently observed copulating which allowed confirmation of sexual identities from mount

positions (male assumed to mount). A distinction was made between mounting (standing on back of mounted bird) and copulating (mounts with tail "tucking" and apparent cloacal contact) to guard against reverse mountings which have been reported for some species (R. Storer personal communication). Only copulations were considered as sufficient confirmation of sex.

Spotting and size estimations were made for pairs of marked individuals of known sex. Three subjective categories for breast spotting patterns were recognized: heavy (numerous spots with a tendency for spots to be large, reaching approximately 3 - 5 mm in diameter); light (few spots with a tendency for spots to be small, approximately 0.5 - 1.5 mm diameter) and intermediate (all instances which could not be assigned to heavy or light categories with confidence). Size and spotting evaluations were made only when two birds were in close proximity (within 2 m radius) and engaged in some neutral activity (e.g., feeding, preening, sleeping). Relative size estimations involved a simple visual attempt to determine whether one bird was noticeably larger.

Birds were trapped with flush nets (Kagarise 1979) at the nest, by stalking, or with mist nets while

brooding young. Colour bands, U.S. Fish and Wildlife Service bands and color markings (biological dyes, Dixson Redimark) were used to mark individuals. Because colour leg bands were not visible when birds moved through grass or when flushed, additional colour markings were made on the neck and/or flanks of trapped birds. Adults were also weighed (Pesola spring scale, 100 g) and measurements of wing (carpal joint to distal tip of longest primary), bill and tarsus were taken with calipers and ruler (caliper and caliper rule, Lafayette Co.; ruler, Hamilton Bell Co.). Only female weights taken after clutch completion were used. Chicks were also weighed (Pesola spring scales, 10 g, 20 g), measured for tarsus and bill length and banded soon after hatching. Recaptured chicks were also weighed, measured and locations noted.

At each nest the maximum length and breadth and weight were recorded for each egg, which was color marked (Dixson Redimark) for identification of laying and hatching order. Internal diameter of nest depression, maximum depth of depression, height of vegetation over the nest and cover above the nest (percentage of nest structure obscured by vegetation located above the nest) were recorded. Photographs were

taken of each nest, its eggs and surrounding area. Each nest was marked with a numbered stake positioned 1 m away. Internest distances were estimated by pacing. When making observations from a blind, birds were photographed as they approached and left the nest.

When nests were discovered with an incomplete clutch, individual adults were marked at the nest without handling (Moseley & Mueller 1975) to reduce risk of desertion. At some nests only one individual was marked, though multiple visits to such nests allowed determination of whether one or two birds were tending the nest. Observations were concentrated at nests where both individuals were marked early in the season.

Results

Nesting Patterns. In 1979 daily observations and surveys began on 18 May. Spotted Sandpipers were first seen on 23 May when three solitary birds were observed feeding on the shore. On 24 and 25 May, in addition to solitary birds seen feeding along coastal areas, birds were seen feeding in pairs (i.e., two birds moving together in close proximity while feeding) among the

rocks and at times moving into grassy areas further inland and participating in nest searching activities (i.e., two birds walking closely together through grassy upland areas in crouched posture with rumps elevated, head and neck lowered and intermittently scraping ground with feet). A. Nash (personal communication) has observed two female Spotted Sandpipers involved in an interaction which closely resembled a nest searching sequence. On 26 May copulations and associated courtship flights were first observed. By 28 May eight of 14 birds observed during the day were seen nest searching as pairs well upland in grassy areas. The number of birds counted during surveys continued to increase steadily until 5 June when a steady decline in numbers began, suggesting that birds were beginning to incubate (Figure 2). This interpretation is supported by clutch initiation dates (Table 1).

Observations suggest that both sexes arrive at about the same time, in late May/early June and soon form breeding pairs. Owing to the substantial number of unmarked birds, there is no way of knowing if additional birds continued to arrive or if early arrivals moved on later in the season.

Figure 2. Bird counts from daily surveys during 1979 and 1980. Missing data points represent days when fog that restricted visibility to 50 m or less and/or rain persisted until noon.

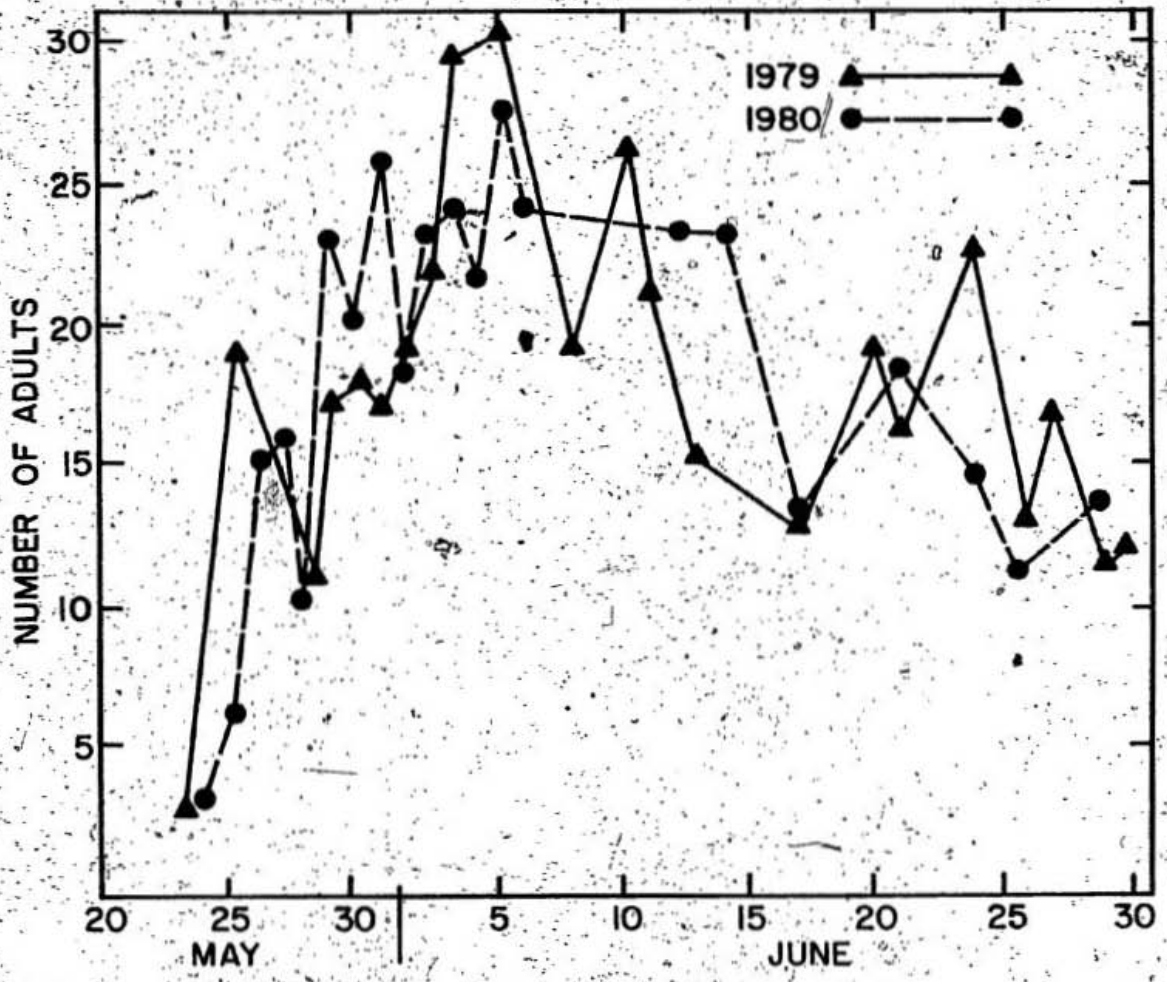

1979
1980
NUMBER OF ADULTS
30
25
20
15
10
5
20
25
30
MAY
5
10
15
20
25
30
JUNE

Table 1

Nesting Records of Spotted Sandpipers on Green Island, Newfoundland during 1979

nest #	female	male	clutch initiation[a]	clutch completion[a]	hatching date	hatching success
1	cm/cb[b]	cm/cb	3 June	6 June	abandoned	
2	---	/ cm[d]	5 June[c]	8 June[c]	1 July	4
3	cm	cm	9 June[c]	13 June	3 July	4
4	cm	cm/cb	11 June	15 June	7 July	4
5	---	---	9 June[c]	12 June[c]	4 July	3
6	cm/cb	cm/cb	10 June[c]	13 June[c]	5 July	3
7	cm	cm	17 June	21 June	11 July	4
8	cm/cb	cm/cb	15 June[c]	18 June[c]	10 July	4
9	---	---	17 June	20 June	11 July	4
10	---	---	11 June[c]	14 June[c]	6 July	4
11[e]	----------				(4 eggs)	
12	cm/cb	---	8 June[c]	11 June[c]	3 July	1
13	cm/cb	cm/cb	11 June[c]	14 June[c]	6 July	4
14[f]	----------				(4 eggs)	

[a] 21 day incubation and 4 day egg laying periods were assumed for estimations when exact dates were not known

[b] cm = colour marked, cb = colour banded

[c] estimated from known hatching date

[d] incubating bird photographed extensively for identification

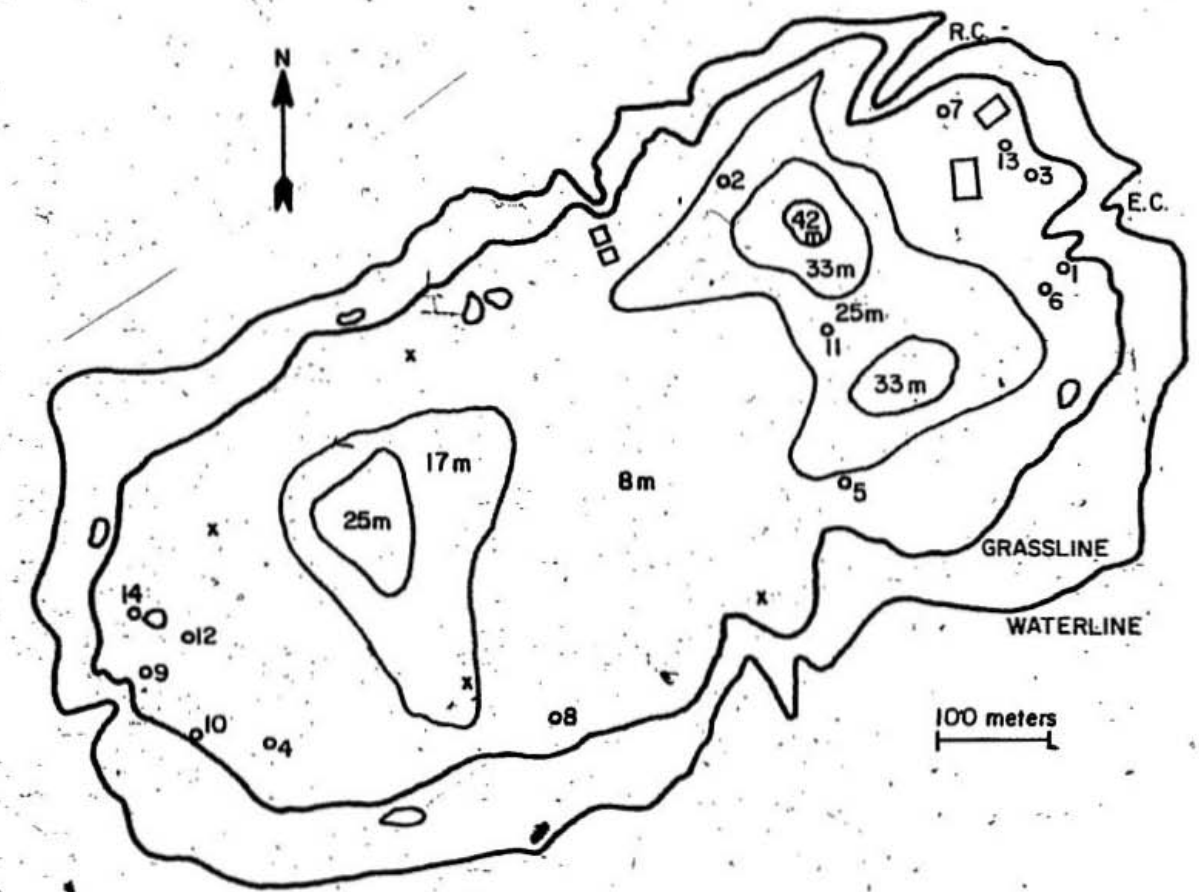
[e] found and accidentally destroyed 24 June

[f] lost to predation 2 July

For seven nests incubation (interval between last egg laid and first egg hatched) required 21.75 days (range = 21 - 23 days). Some nests requiring longer incubation periods (e.g., nest 1/80 took 25 days) showed some signs of disturbance, i.e., eggs were frequently found cold. Because the pattern of nest checks used in this study would tend to overestimate incubation periods, incubation was assumed to require 21 days for calculations (e.g., to estimate clutch completion dates from hatch dates of nests found with completed clutches).

Locations of nests and four additional broods (for which no nests were located) observed during 1979 are shown in Figure 3. The mean ($\pm$S.D.) minimum inter-nest distance (including brood locations from unknown nests as approximate nest locations) was 89.9 $\pm$ 58.3 m. The first known successful nest was initiated about 4 June and completed (4 eggs) about 8 June. The three additional broods from undetected nests were discovered on 3 July (one adult, three chicks), 7 July (one adult, four chicks) and 8 July (two adults, three chicks). Chicks in these broods were estimated to be 24 - 48 hr old when found. The estimated nesting density for

Figure 3. Map of Green Island and nests studied during 1979. Circles indicate locations of nests discovered before hatching. Locations where broods from undetected nests were first discovered are indicated by Xs. Raven Cove (R.C.) and East Cove (E.C.) are indicated.


N
R.C.
E.C.
07
13
03
02
42 m
33m
25m
01
06
11
33 m
17m
8m
25m
05
GRASSLINE
WATERLINE
14
012
09
10
04
08
100 meters

known nests in 1979 was therefore 4.77 nests ha^{-1} (17/3.8). Breeding chronology and hatching success data for nests under observation in 1979 are summarized in Table 1. Additional information on sexual identification and pairing behaviour of birds tending these nests is summarized in Table 2.

To study nest attendance during incubation, most nests were visited at least once or twice daily and incubation by a single individual was inferred only after a minimum of seven nest visits where the same marked and positively identified individual was found on the nest. Most such decisions were based on considerably more data. There is some evidence that females may not incubate regularly but continue to visit a nest intermittently and sit for short periods in the early morning and/or late afternoon (Hays 1972; A. Nash personal communication).

In 1980, daily surveys began on 22 May. On 24 May the first three Spotted Sandpipers were seen feeding along the shore. On 26 May birds were first seen feeding in pairs with intermittent posturing and courtship flights. On 27 May pairs were seen copulating and nest searching in grassy areas. On 28 May an empty nest scrape was found. As in 1979, survey counts showed

Table 2

Pairing Behaviour Observed for Birds at Study Nests, 1979

nest #	copulation	feed together	posture together	nest search	# birds incubate	# birds brood
1	+	+	+	+	abandoned	
2	-	-	-	-	1	N/A[a]
3	+	+	+	+	2	N/A
4	+	+	+	+	2	N/A
5	-	-	-	-	N/A	N/A
6[b]	+	+	+	+	2[c]	2
7	+	+	+	-	2	N/A
8	+[d]	+	-	-	2	2
9	-	-	-	-	N/A	N/A
10	-	-	-	-	N/A	N/A
11	found (4 eggs) and accidentally destroyed 24 June					
12	-	+	+	-	2	N/A
13	+[d]	+	+	-	2	N/A
14	discovered (4 eggs) 29 June; predation 2 July					

[a] N/A = no relevant observations

[b] this was a second nesting attempt

[c] incubation by second bird confirmed late in season

[d] copulation for male observed in 1980

an increase in birds until 5 June when numbers began to decline (Figure 2). During the season evidence of 20 nests was found (17 nests and three broods from undetected nests). General data on these nests are summarized in Table 3 and information concerning sex identification and pairing relationships for birds at these nests is in Table 4. Approximate nest and brood locations are shown in Figure 4.

The shortest distance between any two nests was 37 m (nests 12/80 and 17/80) with a mean minimum inter-nest distance of 82.4 $\pm$ 20.6 m. The estimated nesting density for known nests in 1980 was therefore 5.26 nests ha^{-1} (20/3.8). Inter-nest distances did not differ significantly between the two seasons ($t(36)$ = .501, $p>.10$), and nest density and distribution on Green Island appear quite similar in 1979 and 1980.

Visual examination of the nesting distribution in Figures 3 and 4 suggest that Spotted Sandpipers nesting on Green Island tend to establish nest sites in grassy areas near the shore. To test this impression a rectangular coordinate system with x-axis (n = 215) and y-axis (n = 275) was superimposed on a map of Green Island and random pairs of x and y coordinates were computer generated and used as random nest locations

Table 3

Nesting Records for Spotted Sandpipers on Green Island, Newfoundland during 1980

nest #	female	male	clutch initiation	clutch completion	hatching date	hatching success
1	---	cm/cb[a]	31 May[b]	3 June[b]	28 June	4
2	cm/cb	cm/cb	4 June[c]	7 June	30 June	4
3	discovered (4 eggs) 10 June; predation 12 June					
4	---	cm/cb	10 June	15 June	6 July	4
5	---	cm/cb	7 June[b]	10 June[b]	2 July	3
6	---	cm	8 June[b]	11 June[b]	3 July[b]	3
7	---	cm	9 June[c]	13 June[d]	5 July	4
8	---	cm/cb[e]	2 June[f]	5 June[f]	abandoned	
9	cm/cb	cm	13 June	18 June	abandoned	
10	---	cm	11 June[b]	14 June[b]	6 July	4
11	cm	cm/cb	19 June[d]	22 June[d]	14 July[c]	N/A[f]
12	---	---	15 June[g]	18 June[g]	10 July[g]	N/A
13	cm/cb	cm/cb	14 June[b]	17 June[b]	9 July	4
14	---	cm/cb	---	---	unhatched[h]	
15	cm/cb[d]	---	10 June[b]	13 June[b]	5 July	4
16	---	cm	6 June[b]	9 June[b]	1 July	4
17	cm/cb	cm/cb	discovered (4 eggs) 26 June; predation 2 July			

Table 3. Footnotes.

[a]cm = colour marked, cb = colour banded

[b]estimated from known hatch date

[c]estimated from known clutch completion date

[d]sex based on wing and weight measurements

[e]estimated from embryo examination following desertion

[f]N/A = no relevant observations

[g]estimated from evidence of hatching

[h]no signs of hatching on A.M. 9 July when last observation made

Table 4

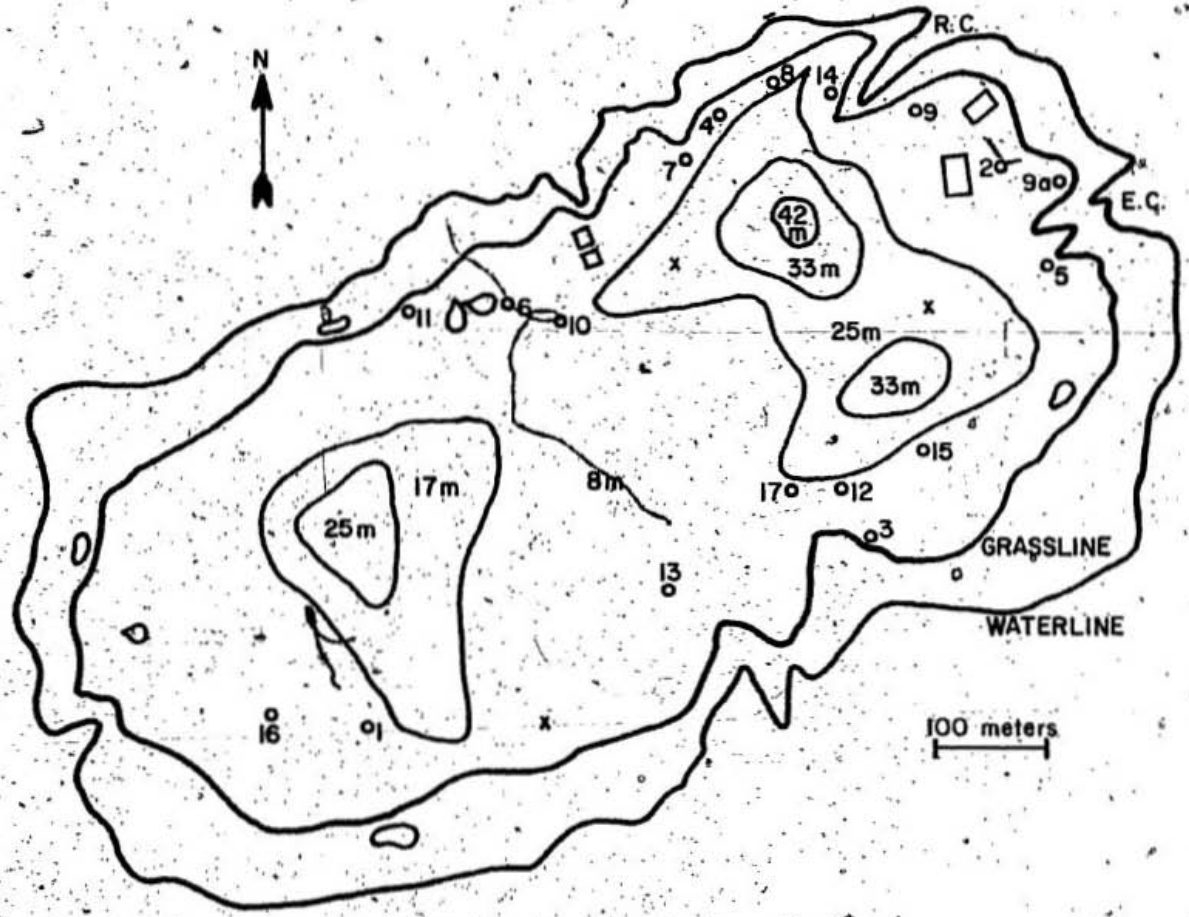
Pairing Behaviour Observed for Birds at Study Nests, 1980

nest #	copulation	feed together	posture together	nest search	# birds incubate	# birds brood
1	-	+	-	-	N/A[a]	N/A
2	+	+	+	+	1[b]	2
3	discovered (4 eggs) 10 June; predation 12 June					
4	-	+	+	+	1	2
5	-	+	+	-	2	N/A
6	-	+	-	-	1	N/A
7	+	+	+	-	2	2
8	N/A	N/A	N/A	N/A	abandoned	
9	+	+	+	+	abandoned	
10	-	+	+	-	1	1
11	+	+	+	+	1	N/A
12	-	-	-	-	N/A	N/A
13	+	+	-	-	2	N/A
14	-	-	-	-	N/A	N/A
15	-	-	-	-	N/A	2
16	-	+	+	-	1	2
17	-	+	+	-	2	N/A

[a] N/A = no relevant observations

[b] only the male incubated until the eggs began to hatch when the female also began to incubate

Figure 4. Map of Green Island and nests studied during 1980. Circles indicate locations of nests discovered before hatching. Locations where broods from undetected nests were first discovered are indicated by Xs. Raven Cove (R.C.) and East Cove (E.C.) are indicated.


N
R.C.
E.C.
14
9
8
4
7
9
2
9
5
42 m
33m
25m
33m
11
6
10
15
17
12
3
8m
17m
25m
13
16
1
GRASSLINE
WATERLINE
100 meters

(points falling on inappropriate nesting substrates (water, rocks, buildings, etc.) were discarded). For each nest location (random and observed), the shortest distance to the shore was measured; actual nest sites were significantly closer to shore than randomly generated control sites in 1979 ($t(26) = 3.18$, $p<.005$), 1980 ($t(34) = 3.35$, $p<.005$) and for both seasons combined ($t(62) = 4.50$, $p<.005$).

Nesting data from 1979 and 1980 (Tables 1 and 3) are compared in Table 5. Table 6 shows the results from nest visits and attempts to determine the number of individuals participating in incubation and brood tending. At all four nests trapped after dark in 1980, males were incubating.

Three of four adult males banded on the island in 1979 returned and nested in 1980. At 2300 h on 11 June O/G-M (M = male) was trapped at nest 1/80. This male had been banded in 1979 when he incubated at nest 4/79 some 97 m away. On 5 June W/O-M was trapped while incubating on nest 2/80. This male was first trapped in 1979 when he incubated at nest 13/79 some 26 m distant. On 21 and 22 June R/A-M was seen copulating with an unbanded female on the NE shore of Green Island. This male nested at the opposite end of the island in 1979

Table 5

Summarized Nesting Histories 1979, 1980

reproductive information	1979	1980	Total
First arrival	23 May	24 May	
Highest survey count (date)	31 (5 June)	28 (5 June)	
Clutch initiation (first/mean/S.D.)	3 June/11 June/4.3	1 June/9 June/4.9	
Hatching dates (first/mean/S.D.)	1 July/6 July/3.4	28 June/5 July/4.6	
# Nests observed	14	17	31
Nests discovered after hatching	4	3	7
# Abandoned nests	2(14%)[a]	2(12%)	4(13%)[a]
$\bar{X}$ Clutch size	4.0	4.0	4.0
% Fledging success[b] (# nests)	91%(11)	83%(10)	88%(21)
$\bar{X}$ Number hatched eggs at successful nests[b]	3.55	3.80	3.67
% Predation (# of nests)	8%(1)	17%(2)	13%(3)
$\bar{X} \pm$S.D. Days incubation (n)	21.4 $\pm$0.65(4)	22.0 $\pm$0.82(3)	21.8 $\pm$0.77(7)

[a] one nest accidentally destroyed

[b] success = at least one young fledged

Table 6

Incubation and Brood Tending

# nests attended by	1979		1980	
	incubation	brooding	incubation	brooding
one adult[a]	1	0	6	1
two adults[b]	7	3	4	5
uncertain #	5	10	3	8

[a] assumed after a minimum of seven nest visits, where the tending bird was marked and positively identified

[b] assumed when two marked birds (or one marked and one unmarked) were observed tending the nest

with a female who was also banded, but no nest for this male was found in 1980. Interestingly the first two nests known to hatch eggs in 1980 (nests 1/80 and 2/80) were tended by males known to nest on Green Island in 1979. Of the four females banded in 1979, none were known to return in 1980. Of the 51 chicks banded in 1979, none were known to return to Green Island in 1980.

Plumage and Size Dimorphism. For Spotted Sandpipers there is a tendency for females to be larger and have more heavily spotted breasts than males (Figure 5). On Green Island, perceived differences in size and spotting were not always reliable indicators of sex: in some pairs both sexes were heavily spotted and differences in size often were not apparent. In addition, "heavy" and "light" spotting categories were not clearly non-overlapping in all instances. Hence, it was necessary to adopt an "intermediate" category for describing some birds. While in some sexed pairs both individuals were heavily spotted and showed no apparent size difference, no pair in which the male was obviously larger or more heavily spotted was observed.

Table 7 shows evaluations of spotting patterns for unmarked birds not known to be associated with any

Figure 5. Example of plumage dimorphism: photograph taken following a copulation where the heavily spotted bird (left) was mounted by the lightly spotted bird.

of the nests under study. In the first category (copulations) sex identification was based on observed copulations (copulations refer to mounts with tail "tucking" and apparent cloacal contact). In all cases, evaluations of spotting patterns were made before copulations were observed. In the second category (judged pairs), birds were assumed paired on the basis of behaviour: feeding in close proximity, posturing and/or nest searching together. The third category (single birds) involved solitary birds that were easly observed and evaluated. The last category is used only to show the proportion of individuals that could not be reasonably described using only heavy and light categories for spotting and suggest the approximate representation in the three spotting categories used. Because individuals in Table 7 were not marked, the frequencies must be viewed with caution. Multiple evaluations were not made at one location as a precaution to minimize repeat evaluations of an individual bird (i.e., observations of marked birds indicated that they could reliably be found in the same location on different days). In the second and third categories evaluations were not made for birds regularly observed at the same locations and sexual identities were not known.

Table 7.

Perceived Differences in Breast Plumage Spotting

Among Unmarked Birds, 1979 and 1980

I	Copulation Observed	
	difference	8
	no difference	3
II	Judged Pairs	
	difference	19
	no difference	5
III	Single Birds	
	lightly spotted	8
	heavily spotted	10
	intermediate	5

During 1979 and 1980, a comparison of spotting and/or size differences between members of breeding pairs with at least one marked individual were made for 16 pairs (Tables 8 and 9). Six pairs showed no obvious spotting differences, and four pairs showed no apparent differences in spotting or size.

For trapped birds weight and wing measurements were used to estimate size. The mean ($\pm$S.D.) weights for nine males and seven females (only marked birds sexed by observing copulations and/or egg laying are included here) respectively are 43.6 $\pm$ 2.3 g (range = 40.9 - 47.6 g) and 46.4 $\pm$ 1.7 g (range = 43.5 - 48.4 g). Females were significantly heavier than males (6% average difference, n = 16, $t(14)$ = 2.14, $p<.05$).

Female wings averaged significantly longer (4%, n = 10) than males' (females 111.3 $\pm$ 0.9 mm; males 106.8 $\pm$ 2.1 mm; $t(8)$ = 3.27, $p<.01$). The cube root of weight can be used to compare weight and linear measurements (Ralls 1976); using this procedure female Spotted Sandpipers for this population averaged 2% larger than males, also a significant difference ($t(14)$ = 2.08, $p<.05$).

It can be noted that the male at nest 2/80 weighed 7% more than the female with which he was paired. This

Table 8

Plumage and Size Dimorphism, 1979

nest #	sex	weight (g)	tarsus (mm)	spotting category	diff.[a]	clutch[c] Weight(g)
3	M	---	---	int.[b]	no	---
	F	---	---	heavy		
4	M	41.5	26.0	int.	yes	---
	F	---	---	heavy		
6	M	40.9	26.5	int.	no	44.0
	F	45.5	28.5	int.		
7	M	---	---	int.	N/A	---
	F	---	---	int.		
8	M	44.5	29.5	N/A	yes	42.5
	F	48.4	26.0	N/A		
12	M	---	---	int.	N/A	34.9
	F	47.0	28.0	N/A		
13	M	42.5	26.5	heavy	no[d]	35.4
	F	45.0	28.0	int.		

[a] presence or absence of a perceived difference in degree of spotting for M/F pair

[b] int. = intermediate spotting

[c] clutch weight given only when female weight is known

[d] M was judged to be more heavily spotted than F on two occasions but the difference was not reliable

Table 9

Plumage and Size Dimorphism, 1980

nest #	sex	weight (g)	tarsus (mm)	wing (mm)	spotting category	spotting diff.[a]	clutch[b] weight (g)
1	M	41.5	26.2	108	light	N/A	---
	F	---	---	---	N/A		
2	M	46.5	26.5	106	heavy	no	36.3
	F[c]	43.5	27.4	110	heavy		
4	M	42.5	27.0	105	int.	yes	---
	F	---	---	---	heavy		
5	M	46.3	27.0	105	int.	no	---
	F	---	---	---	int.		
6	M	---	---	---	heavy	N/A	---
	F	---	---	---	N/A		
7	M	---	---	---	light	yes	---
	F	---	---	---	heavy		
8	M[d]	42.5	27.0	106	int.	N/A	---
	F	---	---	---	N/A		
9	M	---	---	---	int.	yes	29.9[e]
	F	43.5	27.4	110	heavy		
10	M	---	---	---	light	yes	---
	F	---	---	---	heavy		
11	M	43.0	28.0	---	light	yes	---
	F	---	---	---	heavy		
13	M	41.7	27.0	109	heavy	no	40.7
	F	46.4	26.4	112	heavy		
14	M	40.8	27.2	104	heavy	N/A	---
	F	---	---	---	N/A		
15	M	---	---	---	N/A	N/A	38.4
	F[d]	48.0	27.5	108	int.		
16	M	---	---	---	light	yes	---
	F	---	---	---	int.		
17	M	47.6	27.3	110	light	yes	36.8
	F	48.7	28.0	112	heavy		

[a] presence or absence of a subjective difference in degree of spotting for M/F pair

[b] clutch weight given only where corresponding F weight is known

[c] same F attended nests 2 and 9 in 1980 (see text)

[d] sex based on wing and weight measurements

[e] nest abandoned after three eggs laid; weight represents three eggs

female's weight was not taken until the end of incubation (29 June) while the male's was taken six days earlier; this weight difference may be influenced by a tendency for weight loss during incubation (see Ashkenazie & Safriel 1979), though I know of no evidence to support such a trend for Spotted Sandpipers.

For the six breeding pairs for which weights for both individuals were taken, differences ranged from 6 to 11%. In my experience, weight differences of this magnitude are not reliably discernible in the field, especially when the male and female are rarely seen together for comparison once incubation begins. Additional points concerning sexual dimorphism in this species are presented in the Discussion.

Polyandry. Two females were known to pair (i.e., were seen feeding, preening, nest searching, posturing and copulating with a male) with more than one male in 1980. A third instance of polyandry was suspected at another location (owing to a high level of singing, posturing, chasing and related activities during a 2.5 day period), but key individuals at this location were not marked. Nothing resembling these periods of

exaggerated singing, posturing and chasing was observed in 1979. Some case history data are presented here.

W-F: W/O-M and NB. During 1 - 5 June W/O-M was observed feeding, nest searching and copulating with W-F on the eastern end of the island (this male was trapped in 1979 when he incubated at nest 13/79 with a female that was also banded but was not seen in 1980). Their nest (2/80) was discovered on 5 June with two cold eggs. On 6 June W-F was observed preening, feeding and posturing with an unmarked bird (NB: first identified by missing toes on right foot and associated limp when walking) along the shore below her first nest. This same day, W-F and NB were observed nest searching in Raven Cove (Figure 4) at the location where their nest (9/80) was later established. On 7 June (1133 h) W-F completed her first clutch and was subsequently seen feeding, preening, posturing and flying short solitary hover flights (i.e., short flights describing an inverted "U" where the portion of the flight descending from the apix has a conspicuously slowed and hovering character. Hover flights are performed by males and females and are often associated with courtship, i.e., terminate in copulation or mounting.) with both W/O-M and NB in the area near her

nest. For a 3 hr period that afternoon W-F, NB and W/O-M, along with three other birds from neighboring nests, participated in a bout of continuous calling, singing, nest scraping, vigorous fighting and brief flights in the area surrounding nest 2/80. During 8 - 13 June, W-F and NB were regularly seen nest searching, feeding and preening together in Raven Cove. Also during this period W/O-M visited Raven Cove on several occasions to feed at the shoreline and was chased from the area by W-F. NB was first seen mounting W-F on 11 June (no tail tuck) and copulating (tail tuck) on two occasions on 12 June. W-F laid the first egg in her second nest (nest 9/80) on 13 June. W-F and NB continued to associate in Raven Cove until 17 June when the nest was abandoned with three eggs. W-F and NB began to feed together and nest search in the area below her first nest (2/80) at this time and together continued to chase W/O-M when he was in their vicinity. This continued until 27 June when the eggs at nest 2/80 first showed signs of pipping and W-F began to visit the nest to incubate and subsequently care for her young with W/O-M (see section on Posthatch Behaviours).

The events associated with a second polyandrous female can be summarized as follows: On 19 June nest

11/80 was found with one egg and during the next three days the attendant female (R-F) and male (R-M) were marked. With clutch completion (22 June), R-M began incubating at the nest and R-F was regularly observed feeding in the surrounding area. On 25 June the northwestern shore of Green Island surrounding nest 11/80 was characterized by much singing, calling, displaying and intermittent fighting among at least five birds throughout the day. One outcome of this activity was the mounting of R-F by a lightly spotted unmarked bird believed to be a new arrival to the area: all lightly spotted birds seen along the northwest shore had earlier been colour marked and were known to be incubating at other nests.

On 26 June and subsequently R-F was observed nest searching with a lightly spotted unmarked bird 45 m west of nest 11/80 where R-M was incubating. Two nest scrapes were found in this area but no nest discovered. A full copulation between R-F and a lightly spotted unmarked male was observed on 28 June.

Behaviour in Posthatch Period. The longest any family was observed after leaving the nest was 11 days. At nests where all eggs hatch synchronously (i.e., within 8 hr) the young typically leave the nest within

24 hr of hatching. If one or more eggs fail to hatch, incubation may be prolonged and the nest exodus delayed. On Green Island, after leaving the nest the young and attending adult(s) move toward the shoreline nearest the nest. The grassy interior portions of Green Island end abruptly at the rocky shoreline creating a sharp division between these two habitats. Young typically linger near the grass-rock interface and feed almost exclusively in the grass during the first days after leaving the nest. Feeding excursions into rocky areas increase in frequency on subsequent days. The greatest distance a family was known to travel from their nest before reaching an area where they lingered near the shore was 13[illegible]m. Some such movements involved only 15 - 20 m.

Four broods closely observed after leaving nests were almost always accompanied by an adult. The attending adult typically stationed itself on some elevated point overlooking the area where the young fed and called (metalic "toot" notes) at short intervals (3 - 5 sec). When an intruder or potential predator came near, the adult(s) approached and followed the intruder while calling loudly. The young either remained concealed or moved away from the vocalizing adult.

After the intruder left, the adult resumed "tooting" notes.

Broods tended by one adult were typically left unattended only during short periods when the adult left to feed. Broods tended by two adults were virtually always monitored: an adult normally left to feed only when its mate was present. During a continuous 3 hr observation period at nest 2/80 (two attending adults), feeding trips were made every 11.5 $\pm$ 2.3 min on average (range = 7.5 - 17 min). These chicks were left unattended for 9 min. For a comparable observation period at nest 10/80 (one attending adult), the young were left unattended for at least 43 min, and the adult made on average feeding excursions every 8.0 $\pm$ 1.7 min (range = 4.5 - 13 min). Feeding bouts in both conditions lasted for 3 - 4 min. While this comparison is suggestive, more detailed studies are needed to demonstrate if any significant functional differences exist between single and double adult attendance patterns. Adults tending broods alone seem to feed closer to the brood and to watch the area while feeding. For broods with two attending adults, only one adult visited the brood for long periods on some days. For three broods with two attending adults (marked and

sexed), males regularly showed more overt signs of alarm than females when an intruder approached. These males approached the intruder while calling loudly and often performed distraction displays. At such times the female was often seen feeding nearby without overt concern. The reverse pattern was not observed.

No adult was observed feeding at locations < 50 m from young. For four broods that were closely watched, the attending adult left the brood at regular intervals to feed at locations estimated to be 150 - 300 m distant. On some occasions adults were seen feeding at locations 50 m from young in rocky shore areas; the young however did not venture more than 5 m into the rocks from the grassline at that time.

Gulls (Larus argentatus, L. marinus) resting on the rocky shore areas at Green Island were often attracted to areas where adult Spotted Sandpipers tended young. On cold, damp days this presented a special problem: when gulls intruded adults could not visit or brood their young which often vocalize when unattended in these conditions. Gulls easily localized these calls and preyed on young sandpipers.

Aggression. Aggressive interactions were observed infrequently on Green Island and occurred in various

contexts which will be described. Defense of nesting territories or feeding areas was not apparent and aggressive interactions judged to be related to territory defense represented a small proportion of all observed aggressive behaviour. Use of widely overlapping feeding areas without conflict was frequently observed.

During 1979 and 1980, 32 aggressive interactions were observed. These involved chasing, lunging, pecking and/or fighting (reciprocal aggression). Four of these interactions have been discarded from consideration because of the likelihood that the individuals involved were members of a breeding pair.

Defense of territories or feeding areas accounted for 22% (6) of the aggressive interactions. Typical examples involved incubating birds chasing other individuals that fed near their nest, or marked individuals chasing other birds from areas where they regularly fed.

About 29% (8) of the aggressive interactions involved what were known or believed to be (on the basis of size, spotting and behaviour) one-female-multi-male groups. Aggression in such groups (with one exception) involved chasing, posturing and/or

fighting between males, while the female remained uninvolved or fed nearby. The occurrence of such interactions suggests there was an excess of males on Green Island, though this could not be objectively verified. In connection with these one-female-multi-male groups, it may be relevant that in 1979 and 1980, 80% (4/5) and 96% (22/23) of the observed aggressive interactions respectively involved interactions among groups of three or more individuals. Seven of the 23 aggressive interactions observed in 1980 involved aggression between W-F and her mates (W/O-M and NB) following the completion of her first clutch (nest 2/80) (see section on Polyandry).

There were two occasions in 1980 which fit Oring and Knudson's (1972:65-67) description of "post-laying sexual resurgence". The first involved when W-F completed her first clutch (nest 2/80) and the second involved R-F at nest 11/80 (see section on Polyandry). (1) The sexual resurgence with W-F involved interactions between as many as six birds with much associated singing, posturing and fighting. Because these interactions occurred over a large area with thick grassy substrate, which obscured the birds at times, all of the interactions could not be specified

and were counted as one aggressive event. (2) In the second interaction, R-F did not begin what appeared to be a period of sexual resurgence immediately following clutch completion. She laid her fourth and final egg in nest 11/80 on the evening of 22 June and her mate (R-M) took over incubation duties. The area remained quiet until 25 June (0645 h) when an unmarked bird (believed to be a new male to the area) was seen associating with R-F who then sang and postured almost continuously. At least seven different birds became involved in the posturing, song exchange and fighting which subsequently continued through the morning and resulted in a mount and copulation between R-F and the new male.

Five interactions in which the nature of the aggression and/or relationship between the participants was uncertain were also recorded.

Discussion

Nesting Patterns and Territoriality. Territorial behaviour has been reported for both female and male Spotted Sandpipers (Emlen & Oring 1977; Oring & Maxson 1978). Oring and Knudson (1972) also reported having mapped territories for their lagoon population by

noting zones of conflict between adjacent pairs. For their island population, Oring and Knudson (1972) reported that territorial boundaries were never firmly established, though this was attributed to high nesting density and prolonged disputes over boundaries. The birds in this island population, however, were not individually marked. Miller and Miller (1948:560) studied an insular population of breeding Spotted Sandpipers and reported that birds shared overlapping feeding areas and "no territorialism was apparent," although their birds also were not individually marked. Hays (1972) did not mention territories as such but referred to "ranges", where birds were regularly observed feeding and displaying. H. Hays (personal communication) observed that aggressive interactions among Spotted Sandpipers nesting on Great Gull Island off Long Island, New York, seemed to occur only during the first few days after the birds arrived; disputes were settled quickly and nesting followed. In explaining the spacing patterns and social organization of Spotted Sandpipers, the territorial behaviour described by Oring and Maxson (1978) and the "ranges" mentioned by Hays (1972) provide two alternative models which differ in several important ways.

Oring and Maxson (1978) and Emlen and Oring (1977) treat polyandry in Spotted Sandpipers much like territorial polygyny (Verner & Willson 1966; Oring 1969) with sex role reversal, i.e. females are territorial and control access to resources essential for reproduction and males selectively mate with females controling high quality territories (see also Graul et al. 1977). When polyandry occurs, males are territorial and apparently partition recources controlled by their mate. Primary males may be expected to interfere when subsequent males attempt to mate with their female. While Oring and Maxson (1978) have stressed the importance of territorial interactions for Spotted Sandpiper mating systems, they also recognize the potentially important role of male nest site tenacity in this mating system.

Emlen and Oring (1977) used the mating system of Spotted Sandpipers as an example of "resource defense polyandry", i.e. females compete for and defend resources essential for successful reproduction by males. Hays (1972), however, suggested that males are attracted to particular nesting sites or areas and females may defend large areas which include several such sites: Males may prefer to mate with females which

control their nesting area by excluding other females (the mating system of some Jacannas apparently operates this way, Jenni & Collier 1972).

The evolutionary significance of strong nest site tenacity by Spotted Sandpiper males has not been specifically addressed. A large proportion of breeding males return to the same location on successive seasons and tend to establish nest sites near those of the preceeding season (Hays 1972; Oring & Maxson 1978; personal observation). Females also show a tendency to return to nesting areas on successive years, though this trend is not as pronounced as for males (Hays 1972; A. Nash personal communication). Returning females also have a higher probability of occupying a new nest site than returning males (Hays 1972). Similar patterns of nest site tenacity have been reported for females and males of other shorebird species (see Soikkeli 1967; Hilden 1975; Schamel & Tracy 1977). While none of the four female Spotted Sandpipers banded on Green Island in 1979 were known to return in 1980, the small sample size precludes generalization.

Male Spotted Sandpipers returning to previous nesting areas tend to nest earlier than males nesting in an area for the first time (Hays 1972). Nesting

records for male Spotted Sandpipers breeding on Green Island are consistent with this pattern.

Hays (1972) suggested that a lessening of importance of the pair-bond and the increasing importance of attatchment of males to particular nesting sites or geographic areas may be an adaptation which facilitates the development of serial polyandry in Spotted Sandpipers and polygyny in other species. While the resource defense model and Hays' model would produce mating systems that appear similar on a superficial level, several important differences are implied. The resource defense model implies that territorial aggression should be spatially distributed so as to defend resources occurring within a geographic area (e.g., exclusive use, Brown 1975). The occupation and defense of preferred areas should be correlated with the distribution of critical resources and males should mate selectively with females that control territories of superior quality, etc. Preferred areas could be more or less stationary on successive years depending on the distribution characteristics of critical resources. The relevant "critical resources" for this species have not yet been specified. Oring (1982:72) reported that of the factors influencing

female reproductive success, variance was explained primarily by experience and territory size and no consistent week-to-week or year-to-year pattern of interterritorial differences in food availability was evident.

In Hays' model, nest site tenacity by males is an important factor influencing nesting distribution, and females will compete to control areas occupied by males. Hays (1972) described an instance of aggression involving two females which she felt suggested that females, by patroling and defending large areas, keep potential males isolated. Males should occupy similar nesting locations on successive years, and these occupancies may or may not be correlated with distribution of critical resources. Although this model would predict male nest site tenacity, the available information already supports such a trend and any model would need to take this into account. The factors influencing male attachment to nesting locations have not been specified (for some discussion see Soikkeli 1967). Most importantly, any aggression in such a system would tend to occur in situations which challenged the breeding activities of an established pair rather than defense of a geographic location

against any intruder per se. For example, females would exclude other females who were looking for mates but might tolerate females who were already paired or tending a nest, and similarly for males. Some overlapping of feeding areas might also be expected in this system.

While several aggressive interactions suggesting territorial defense were observed among birds nesting on Green Island, such encounters were uncommon and overt territorial behaviour (song advertisment, posturing and aggression) was not a notable factor which influenced social organization. The spatial distribution of aggressive encounters observed on Green Island in no way describe boundaries between adjacent nesting or feeding areas. Other nests were widely spaced and large areas with no sandpiper activity occurred between these nests and their nearest neighbors. Marked individuals were regional in habits and fed regularly along certain coastal and upland areas; however, overlapping feeding ranges were regularly observed. At one location, groups of as many as nine birds were regularly seen feeding together (within a radius of 10 m) without conflict. Where feeding ranges of birds tending adjacent nests shared a

common boarder, residents could regularly be seen feeding in their respective areas - in close proximity on many occasions - without posturing or overt aggression. The spatial and temporal distribution and social context characteristic of most aggressive interactions observed on Green Island suggests these interactions functioned to preserve mating relationships (or "mate defense") among breeding pairs and not to defend breeding territories or feeding areas during egg laying and incubation.

Most observed aggressive interactions involved groups of three or more individuals. The trend among such groups appeared to be for one female to associate with two or more males, one of which was more aggressive and attempted to chase other male(s) when they approached the female. Females in such groups were typically engaged in feeding or preening and for the most part not overtly attending to the males. On two occasions a known pair was approached by an unbanded bird believed to be a sexually active female, and the mated female aggressively chased the intruder. Because the sexual identities and reproductive status of all birds involved in these interactions were not certain, this summary must remain speculative.

Sexual Dimorphism: plumage and size. There appears to be some disagreement in the literature concerning sexual dimorphism in Spotted Sandpipers. Hays (1972:45) describes females as "slightly larger" than males and, "in most cases, have more spotting," though she also noted that first year females are lightly spotted and indistinguishable from males. A. Nash (personal communication) has also found this pattern. Oring and Knudson (1972) reported that female Spotted Sandpipers are larger and more heavily spotted than males and relied on perceived differences in size and spotting to sex unmarked individuals in their island population.

For Spotted Sandpipers nesting on Green Island, differences in degree of spotting between the sexes were not always obvious and breeding pairs were noted where the female and male were judged to be similarly spotted. No pair was observed where the male was clearly more heavily spotted than the female, though this has been reported elsewhere (A. Nash personal communication). Because first year females may be lightly spotted and indistinguishable from males, the presence of first year females in a population would tend to bias estimates of sex ratio towards a higher number of males (as reported by Oring & Knudson 1972)

when sexing is based on perceived spotting and size differences.

In a discussion of mating systems, Wittenberger (1979) has suggested that a sex ratio skewed towards excess males is correlated with the number of polyandrous females in a population and with the number of successive mates obtained by these females and cites Oring and Knudson's (1972) study as the only evidence for this. It is suggested here that methods used to estimate sex in their study are open to question. In addition, more recent reports now indicate that the sex ratio for this population is balanced (Oring 1982).

Some controversy exists as to the best method of estimating size in birds generally (Amadon 1943; Jehl 1970; Ralls 1976). Both weight and linear measurements have been used to estimate size and sexual dimorphism in other species (see Ralls 1976). Females nesting on Green Island are 6% heavier than males (Table 10). Mayfield (1979:27) reported a mean weight of 46.7 g for 10 breeding season female Spotted Sandpipers from weights recorded on specimen labels in the University of Michigan Museum of Zoology; this figure agrees well with that of the Green Island population. Females on Green Island had 4% longer wings than males.

Some comparative data on male and female Spotted Sandpiper weights are given in Table 10. For the three samples where average weights for both sexes are given (Minnesota, New York, Newfoundland), estimates of sexual dimorphism based on weight vary considerably (24, 15 and 6% respectively). In addition, while Maxson and Oring (1980) reported no overlap for female and male weights in their Minnesota population, Nash and Cottrell (submitted) found considerable overlap (see Table 10). How accurately these estimates reflect true differences in size dimorphism between populations is uncertain due to differences in measurement technique. Maxson and Oring (1980) used only weights from birds trapped within two days of arrival at the breeding area whereas, Nash and Cottrell (submitted) did not impose this restriction on their samples. If this restriction is imposed on Nash and Cottrell's data the sample is too small to allow meaningful comparison.

A number of factors that might contribute to the discrepant estimates of size dimorphism in Table 10. One possibility, that differences are due to geographic variation, cannot be evaluated conclusively because of

Table 10

Average, S.E. and Range of Weights (g) for Female and Male Spotted Sandpipers and Estimated Size Dimorphism

Location:	Minnesota[a] 47-07 N 94-22 W	New York[b] 41-12 N 72-07 W	Newfoundland[b] 46-15 N 56-01 W	--- --- ---
Females	47.1	47.4[c]/46.0[d]	46.4[e]	46.7
S.E.	---	3.30	1.72	---
range	50 - 43	54.9 - 44.0	48.7 - 43.5	---
(n)	9	7	7	10
Males	37.9	41.3	43.6	---
S.E.	---	2.08	2.15	---
range	41 - 34	44.3 - 38.0	47.6 - 40.9	---
(n)	8	8	9	---
Estimated Dimorphism (% female larger)	24%	15%[c]/11%[d]	6%	---
Source	Maxson & Oring (1980)	Nash and Cottrell (submitted)		Mayfield (1979)

[a] birds weighed within first two days at breeding ground

[b] birds trapped throughout season

[c] three of these females laid eggs within 12 hr after weighing: to correct, the average weight of one egg from that female's clutch was subtracted from her measured weight

[d] average weight without the three laying females (n = 5)

[e] females weighed after clutch completion, i.e. no females laid eggs within 5 days of measurement; male weights taken during early incubation

differences in measurement techniques used (above). Seasonal differences in the weight ratio of the sexes (which may affect the sexes differently, Ashkenazie & Safriel 1978) and weight changes associated with changes in reproductive condition could also contribute to observed differences (see Amadon 1943; Ralls 1976). If one particular measurement of sexual dimorphism (e.g., weight) proves to be contingent on measurements obtained during a brief interval during the breeding season, it will then be necessary to ask if what is being measured realy reflects sexual dimorphism and if such measurements are useful for predicting sex. Considering the number of factors which can influence weight measurements, and that these factors tend to influence female weight more than male weight, the agreement for estimates of average female weight are impressive. Equally impressive is the large and unexpected variation in estimates for average male weight.

Emlen and Oring (1977) reported that female Spotted Sandpipers are 25% larger than males and attributed this difference to sexual selection. The Minnesota data (Table 10) are presumably the basis for this estimate of 25% larger female size (Maxson & Oring

1982). Two conditions - assortative mating and a selective advantage to mating pairs - must be fulfilled if an evolutionary event is to be ascribed to sexual selection (Fisher 1958:150). As far as I am aware the existence of these conditions has not been demonstrated for any population of Spotted Sandpipers. If sexual selection is responsible for larger female size in Spotted Sandpipers, female size should be positively correlated with reproductive success. In addition, the insular variability demonstrated for different breeding populations for this species (Table 10) might be correlated with the degree of polyandry exhibited in different populations. More attention should be given to possible factors influencing variability in male weight as the differences in estimates of sexual dimorphism (Table 10) result from differences in average male weights for these samples.

The lack of agreement for estimates of size dimorphism in Table 10 may suggest that weight is not a good overall indicator of sexual dimorphism for this species and that multiple indices of size should be used. Some data indicate that wing measurements may be a better predictor of sex and allow better estimation of size dimorphism for this species (H. Hays personal

communication; A. Nash personal communication). While plumage markings and size measurements may be helpful for identifying sex of Spotted Sandpipers in the field, such identifications must be interpreted with caution, and more data are needed to assess the reliability and variability of different measurements available for predicting sex.

An adaptive explanation(s) for this female-larger trend among Spotted Sandpipers and other shorebird species remains unclear. Selective pressures for sexual dimorphism with respect to size in birds and mammals has been discussed elsewhere (Selander 1972; Ralls 1976). Several plausable arguments relating female aggression with sexual dimorphism in the existing social system of Spotted Sandpipers have been suggested (Hays 1972; Oring & Maxson 1978).

Sexual selection has been a dominant theory in research on sexual dimorphism (e.g., Murton & Westwood 1977). Emlen and Oring (1977) noted that behavioural and size dimorphism in females increases with the intensity of sexual selection and mention size dimorphism in Spotted Sandpipers as an example. It should be noted, however, that females are slightly (1 - 5% based on wing measurements) larger in all 15

monogamous sandpiper species reviewed by Pitelka et al. (1974) who considered this female-larger pattern to be the primitive arrangement. Selander (1972) also suggested that the female-larger trend among Phalaropes (Wilson's Phalarope, Phalaropus tricolor, females are 26% heavier than males) did not represent a "reversal" as this is the prevalent trend among shorebirds.

The tendency towards larger females among shorebirds suggests that some more general factors associated with their breeding ecology and reproductive physiology may be involved. As a group, shorebirds are ground-nesters which produce large eggs and precocial young and often lay replacement or multiple clutches in rapid succession as an apparent adaptation to high predation and short arctic breeding seasons. Larger female size (and/or reduced clutch size) may be an adaptive strategy to reduce physiological stress associated with egg production (Lack 1968; Oring & Knudson 1972; Selander 1972; Graul 1973; Parmelee & Payne 1973).

Just what constitutes an increase in female size (or a reduction in clutch size) remains unclear in the literature (Murton & Westwood 1977). Oring and Knudson (1972) listed Spotted Sandpipers as a species having

reduced clutch size though no criteria were given. Ross (1979) demonstrated that for species laying multiple clutches, females tend to show an increase in body size and a reduction in clutch size. His analysis however treated multiple clutching species collectively using non-parametric analysis, making evaluations of clutch size reduction for any one species not possible. The general approach for such an evaluation would involve a comparison of relative egg weight (egg weight/female body weight) and relative egg production (clutch weight/female body weight) for Spotted Sandpipers and related shorebird species which do not regularly produce replacement clutches.

Hilden (1975), using Spotted Sandpiper data reportedly obtained from Oring, estimated the relative egg weight and relative egg production for Spotted Sandpipers to be 17.1 and 68% respectively. Hilden compared these figures to three small European Tringa species (some classifications include Spotted Sandpipers in this genus, Hilden 1975), the Common Sandpiper T. hypolcucos, Wood Sandpiper T. glareolad and Green Sandpiper T. ochropus, which have relative egg weights of 26.0, 22.5 and 19.4% respectively, and

concluded that Spotted Sandpipers have considerably smaller eggs.

A consideration of available measurements for Spotted Sandpiper egg and female weights suggest that the measurements used by Hilden are not representative for this species (Table 11). First, Hilden's (1975) 51.5 g estimate for female weight is 1.5 g more than the largest given for this species weight range by Maxson and Oring (1980:237), and the 8.8 g egg weight is 0.7 g less than the reported mean (Maxson & Oring 1980:238). Estimates of relative egg weight and egg production from other sources (see Table 11) indicate that female Spotted Sandpipers produce clutches comparable in size to other related shorebird species and are not "reduced" in size. Maxson and Oring (1980:238) noted that the ratio of Kcal required to produce an egg/BMR for Spotted Sandpipers is greater than that given for all but one of 14 species of various taxa listed by King (1973).

The idea that egg production may physiologically stress the female has frequently been involved in explaining the evolution of polyandrous mating systems (Oring & Knudson 1972; Graul 1973). In particular, a

Table 11

Relationship Between Female Body Weight, Egg and Clutch Weight (g) for Spotted Sandpipers

egg weight	female body weight	relative egg weight[a]	relative egg production[b]	source
9.7	46.4	20.9	84	Present study
9.5	47.1	20.1	80	Maxson & Oring (1980)
9.0	46.7	19.3	77	Mayfield (1979)
8.8	51.5	17.1	68	Hilden (1975)[c]

[a]egg weight as a percentage of female body weight

[b]clutch weight as a percentage of female body weight

[c]data obtained from L.W. Oring

female's energy reserves may be so depleted following egg-laying that additional parental investment would significantly decrease her inclusive fitness, and selection might favor desertion by females and assumption of all parental duties by males (Graul et al. 1977). This idea remains to be substantiated and some evidence to the contrary exists for Spotted Sandpipers (see below). Moreover, Oring (1982:73) has now concluded that the strain of laying multiple clutches for some female Spotted Sandpipers must not be excessive as they breed for at least eight years, as do males. This observation holds however for females that are now larger and a similar investment in egg production by smaller females (i.e., the same size as males) may have been stressful. Ralls (1976) has suggested that for those species of mammals where the female is larger than the male, large mothers are likely to produce large babies with better chances of survival than small babies.

Polyandry. In a comparative review of sandpiper social systems Pitelka et al. (1974) recognized two general categories for reproductive

stategies used by the calidridine species they discussed. (1) The "conservative" strategy employed by the majority of calidridine species is characterized by monogamous matings with persistent residence of both pair members throughout most of the season. Breeding pairs establish evenly spaced territories that provide adequate breeding resources for adults and brood even when breeding conditions are not favorable. This may be accomplished by occupying large territories when food is more limited or small territories in favorable nesting habitat and obtaining additional food from communal feeding areas nearby. This strategy is conservative because reproduction tends to be constant with each pair raising one brood per season independent of fluctuations in breeding resources. (2) The "opportunistic" strategy includes mating strategies evolved to maximize reproductive success when breeding conditions are favorable. Species included in this category tend to occupy small territories packed into more productive marshy habitat, balancing the risk of breeding failure in the event of adverse weather

against the probability of a very successful breeding season if conditions are favorable. This category is more diverse than the conservative category and includes mating systems Pitelka et al. (1974) have called serial polygamy, polygyny and promiscuity. Of interest here is the serial polygamy sub-grouping which includes mating systems containing elements of both polyandry and polygyny.

The serial polygamy sub-grouping is distinguished from other mating systems in several respects: The occurrence of multiple clutches and incubation of each by a single adult distinguishes this mating system from the conservative strategies and incubation by males differentiates it from other opportunistic mating strategies. Females lay two successive clutches, each of which is incubated by a single adult. Pair relationships may include: (i) persistent bonding between members of a pair with the first clutch being incubated by the male, the second by the female; (ii) a female may form a series of temporary pair-bonds with different males, laying a clutch which is incubated by the first male and, after association with a second male, a clutch which the female or both sexes incubate. Examples of serial polygamy given by Pitelka et al.

(1974) include: Temminck's Stint, Calidris temminckii; Little Stint, C. minuta; Sanderling, C. alba and Spotted Sandpipers.

Some degree of emancipation from incubation and nest related activities is necessary for a female to mate with multiple males. A central question in understanding polyandrous mating systems is to identify the selective pressure(s) that make it adaptive for males to assume more responsibility for nest related activities or females to assume less. Nest attendance and brooding by one adult is common among shorebirds. Several factors which would select for attendance by one adult (sex not always specified) have been hypothesized: (i) early departure of one adult to reduce food competition between adults and young; (ii) departure of one adult may make the nest less conspicuous to predators and (iii) energetic costs of egg production may weaken the female such that further participation in nesting activities would be detrimental to her. Observations of Spotted Sandpipers nesting on Green Island do not suggest any clear connection between any of these factors and uniparental care.

Several authors have suggested that the early departure of one individual from the nest area would reduce the rate of food consumption in that area, leaving more food for the tending adult and later for the young (Jenni & Collier 1972; Selander 1972; Pitelka et al. 1974). Given the facility of flight and limited movements of the young, it is difficult to see why adults could not solve this problem simply by feeding at short distances from the nest or young to avoid potential problems associated with food competition rather than leaving the breeding area completely. When two birds tend a nest or young, the off-duty bird could reasonably be expected to commute greater distances and feed longer (hence further reducing food competition) than when a single bird tends the nest. On Green Island, adults tending broods were never seen feeding at areas where the young were known to be feeding. Rather, at frequent intervals adults made trips of 150 - 300 m to feed. This was true for broods tended by one or both parents. In the latter case an adult was virtually always in attendance with the brood. A similar pattern was observed for Spotted Sandpipers nesting on Great Gull Island, New York (A. Nash personal communication). Ashkenazie and Safriel (1979)

reported that adult Semipalmated Sandpipers also feed away from their young. These observations suggest that adults may avoid food competition with their young by feeding at areas adjacent to their brood yet still remain at the breeding grounds.

One way to reduce the risk of nest predation would be to reduce the number of nest exchanges or periods away from the nest by solitary incubators. It is difficult to conceptualize why two birds could not deal with this problem more effectively than one. On Green Island, I have no record of seeing two Spotted Sandpipers together at a nest after clutch completion. At nests where two birds incubated, relieving mates typically called from distances of 30 - 50 m and the incubating bird would promptly leave the nest before the arriving bird approached by a round-about route. It also seems probable that nests with two attendants would require fewer nest exchanges than nests with one attendant since off-duty birds would have more time for feeding.

For some species where the female "deserts" soon after clutch completion, it has been suggested that energetic demands associated with egg production may strain or weaken the female such that she must forgo

the energy demanding task of incubation (Nethersole-Thompson 1973; Graul et al. 1977; Wittenberger 1979). There is some evidence however that male aggression is the proximate mechanism for female "desertion" in some of these species (Graul 1973; Bruning 1974; Kistchinski 1975; Ashkenazie & Safriel 1979). Oring and Knudson (1972) noted that certain female Spotted Sandpipers showed a sudden surge of sexual activity following clutch completion and became involved in extensive singing and aerial advertisment for several days. They felt that these females showing an increase in post-laying sexual activity would be likely to mate with additional males when available.

On Green Island, both females who were known to mate with multiple males showed increased sexual activity, singing, posturing and aggression shortly after clutch completion. While this observation does not prove that females were not physiologically weakened by egg production at some earlier time in evolutionary history or under some other set of environmental conditions, it is contrary to the idea and suggests that at least some female Spotted Sandpipers are not physiologically strained or weakened as a consequence of egg production. Some recent reports

of Spotted Sandpiper reproductive histories indicate that females breed for as many seasons as males leading some to think that egg production is not energetically costly for this species (see section on Sexual Dimorphism). In addition, the observation that a period of sexual resurgence for one female on Green Island did not follow clutch completion immediately but when an available male arrived in the area suggests that the presence of an unattached male(s) may be necessary for a resurgence of sexual behaviour.

Pitelka et al. (1974) discussed the added advantages to young of having two attendant adults: for periodic brooding, leading young to feeding areas, warning young of approaching predators and performing distraction displays. For Spotted Sandpipers nesting on Green Island, the attending adult typically stood on a rock or other prominence overlooking the area where the chicks fed. The adult "tooted" at regular intervals during which the young fed. With the approach of a gull, raven or other intruder, the adult sounded loud calls which prompted young to hide in vegetation or under rocks until "toot" notes resumed. Adults also performed distraction displays in response to approaching intruders, brooded their young at night and

frequently during cold weather. When a female pairs with an additional male(s), the primary male may lose her assistance in providing parental care and this would be one reason a primary male would interfere when subsequent males attempt to mate with his female. An adaptive value for these forms of parental investment remains to be demonstrated for Spotted Sandpipers.

There are still a number of problems concerning the classification of polyandry and mating systems generally which need to be recognized. Wittenberger (1979) defined "true polyandry" as a mating system in which one female is the exclusive mate of several males. Jenni and Collier (1972) define "true polyandry" as a mating system with one female being mated simultaneously or having simultaneous pair-bonds with more than one male. Graul et al. (1977) define polyandry as a system where a female forms pair-bonds (not defined) simultaneously or sequentially with more than one male, and males assume most or all of the parental duties. These general definitions would apparently include the mating systems of the Tinamous (Tinamidae) and Greater Rhea (Rhea americana) whose mating systems Emlen and Oring (1977) considered specialized cases of polygyny coupled with male

incubation. Jenni (1974) has described the Greater Rhea as "polygynous-polyandrous", and polyandry in the Tasmanian Native Hen (Tribonyx mortierii) appears to be a unique form of cooperative breeding among genetically related individuals.

The important distinction in all of these cases concerns the special relationship between members of a reproductive pair, collectively referred to as a "pair-bond", and whether polyandrous females maintain pair-bonds with multiple males simultaneously or bond sequentially in non-overlapping relationships. Although the concept of pair-bond has become a key concept for classifying polyandry and other mating systems, the term has been widely used without definition or the definitions provided are so amorphous that the necessary distinctions cannot be made. For example, Jenni (1974) suggested that most vertebrate mating systems can be classified in terms of the number of individuals with which one individual forms pair-bonds. After mentioning the difficulties of precisely defining the term pair-bond and making comparisons of bonding relationships across species, Jenni restricts his use of the term to mean "that a male and a female copulate with one another." The utility of this definition

quickly breaks down, when Jenni (1974:130) defines promiscuous systems as those where no pair-bonds are formed. Selander (1972) introduced a classification scheme which emphasizes the temporal duration of pair-bonds to distinguish between different mating systems. Selander (1972) also acknowledged the difficulty of defining pair-bond, though for purposes of using his scheme for classifying mating systems he makes no suggestion as to how temporal duration of these bonding relationships should be measured. As another example, Brown (1975) has used the term "mated", "mates" and "pair-bond" without definitions in his classification of mating systems. Wittenberger (1979) embraces the terminology of Selander (1972) and in distinguishing between successive and simultaneous polyandry, introduces the term "acquire" which is not defined: polyandrous females acquire their mates in temporal succession or all at the same time. On what basis are such distinctions to be made?

In order for researchers to compare observations of reproductive behaviour and to test the utility of the concept of pair-bonds in classifying mating systems, the criteria used and assumptions made concerning the formation, maintenance and termination

of bonding relationships must be made explicit. Some researchers (Hays 1972; Howe 1975; Schamel & Tracy 1977) have attempted this. If the concept of pair-bond cannot be usefully employed in the classification of mating systems, alternative classification schemes should be considered (e.g., Ralls 1976:922; Emlen & Oring 1977). Although alternative criteria for defining mating systems have been proposed, these new criteria may still incorporate the pair-bond concept to distinguish between some mating systems (see Introduction).

Female Spotted Sandpipers are normally considered to be serially polyandrous because they associate with two or more males successively, leaving earlier males to incubate after clutch completion and sharing incubation with their final mate (Hays 1972; Oring & Maxson 1978). Oring and Maxson (1978) reported a nesting history for one female Spotted Sandpiper which suggested to them that she maintained pair-bonds with multiple males simultaneously. This female was observed courting and copulating with a second male on dates which overlapped the period when she was still laying eggs for her first mate. After clutch completion she continued to incubate at the nest of her first male

while continuing to consort with her second male. The following season this same female returned to the nest of a first male to brood his young during several days when she was also seen copulating with her third male. Oring and Maxson (1978) felt that this indicated strong simultaneous bonding affinities between the female and her first ("through his clutch") and third males. Using these criteria, one female nesting on Green Island (W-F) would be classified as simultaneously polyandrous: W-F fed, preened, postured and nest searched with a second male (NB-M) before completing her clutch for her first male (W/O-M). She also returned to share incubation with her first male when his eggs neared hatching and subsequently shared in brooding activities.

Interpretation of the pair-bond relationship for W-F and W/O-M is complicated by the observation that on seven occasions while W-F consorted with her second male and before returning to incubate at her first nest, she chased and behaved aggressively towards W/O-M when he approached her in what were apparent attempts to feed with her. These aggressive interactions cannot be explained as territorial interactions as they occurred in Raven Cove (where W-F and her second mate

had their nest) and at the area below W/O-M's nest where he fed throughout the summer. When W-F returned to help W/O-M with his young the pair stood, postured and preened together though the frequency of these behaviours seemed reduced relative to the pre- and egg-laying periods. No behaviours suggesting a pair-bond were observed between W-F and W/O-M during the period from clutch completion until W-F returned to incubate with him. A problem then is not to operationally define the onset of a pair-bond relationship for this pair but to measure its duration and strength. Additional distinctions between attachments to an individual (pair-bond) and to a territory, nest or brood, need to be made, if such distinctions are possible.

Hays (1972) reported a polyandrous female who, after producing a clutch for her second male, provided a replacement clutch for her first male after he lost his first set of eggs. Schamel and Tracy (1977) studied Red Phalaropes (Phalaropus fulicarius) and noted one polyandrous female who, four days after completing a clutch with a second mate, returned to her first mate and fed at times with him. They suggested that bonding with a second mate does not always imply that a

female's bond with her first male is broken. Detailed observations of pair-bond relationships between polyandrous female Spotted Sandpipers and males in different breeding conditions are necessary before conclusions can be drawn concerning the strength, duration and fluctuations of these relationships.

While it would appear that polyandrous matings are a regular feature of Spotted Sandpiper reproductive behaviour, the important factors favoring the ontogeny and evolution of this mating system remain unclear. For example, the prominence of territorial behaviour seems to vary considerably between populations where polyandry has been found to occur. Meaningful estimates of food resources within a given area for members of this opportunistic species would be informative, though difficult to derive (see Appendix 1).

Summary

Two individually marked female Spotted Sandpipers each mated with two males on Green Island, Newfoundland. One of these females mated simultaneously with her two males according to pair-bonding critera

suggested by other researchers. These results suggest that polyandry in Spotted Sandpipers is widespread.

The use of pair-bonding relationships, for which no operational definition is available, to distinguish different mating systems seems inadequate. Even with recent attempts to establish alternative criteria to classify mating systems, pair-bonding characteristics remain the primary criteria for distinguishing between simultaneous and sequential polyandry, and researchers need to be more precise in defining pair-bonding behaviour.

Several results were unexpected and conflict with some previous reports. Most notably, sexual dimorphism based on perceived differences in size and plumage markings did not provide a reliable means of determining sex for this population. More direct measurement of wing and weight from this population indicate that average size differences are significantly less than some reports have suggested. Additional data reviewed here suggest that average size differences for this species may vary geographically and be less than what is generally reported as typical for this species. In addition, it was found that earlier reports suggesting that clutch size for Spotted

Sandpipers is reduced were based on gross interspecific comparisons using extreme egg and female weights. More representative measurements indicate that clutch size is not reduced for this species. Finally, defense of territories/resources and aggressive behaviour was not an obvious factor influencing social organization in this population. The importance of territory defense for this species may vary between populations and with local breeding conditions.

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Appendix I. Food and Feeding Behaviour.

Limited observations indicate that feeding habits of Spotted Sandpipers nesting on Green Island are opportunistic and an accurate assessment of food resources for this species would be difficult. Feeding was most frequently observed at or near the waterline among marine vegetation and ephemeral rock ponds which occur there. Birds feeding in such areas typically collected food items at short intervals (4 - 7 sec); positive identification of these foods was not possible.

During high tides or when waves covered these areas, birds fed higher in rocky coastal areas or moved to grassy upland areas. In these areas birds were observed eating cryptic spiders and moths which rest on rock surfaces warmed by the sun. Crane flies (Tipulidae) were also taken in grassy areas; these insects were often large and required extensive handling before consumption. A small periwinkle (Littorina) was also taken from rocky areas. Small Mysid schrimp (Neomysis americana) were taken in small semi-permanent brackish ponds that occur in higher rocky areas. On several occasions birds were seen probing with their bills in exposed peat at upland

areas and consuming items taken there. Many small excavations were found in these areas. It was also common to see incubating birds eating insects which passed within reach, suggesting that food was abundantly dispersed over the Island. I found no evidence suggesting starvation of young birds as reported by A. Nash (personal communication) for her New York population.